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Main Lines of Evolution in Equisetum—II

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From the primitive *xylochaetum-giganteum* type, with its large, perennial, branched stems, banded stomata, and apiculate cones, another prominent branch or group is derived, the *Equiseta aestivalia.* The stems are annual with prominent whorls of branches and the cones are without a point. The stomata are scattered in broad bands and the sheaths are rather primitive with persistent teeth. *Equisetum fluviatile* L. is the lowest species of this group, followed by the much smaller *E. palustre* L. in which the whorls of branches are much less prominent and often irregular, frequently appearing bushy. The cavities in the internodes of the latter species are much reduced and the sheaths are ampliated, a condition probably retained from the ancestral type. The large branches at least, of the whorls are hollow. These species also show a more or less prominent peduncle at the base of the cone, which is true of all the higher Equiseta. The other two members of the group, *E. diffusum* D. Don and *E. bogotense* H. B. K., are still more extreme, having solid branches, and in the latter species the ridges of the main stem are only four to nine. *E. diffusum* often has solid, main stems but sometimes

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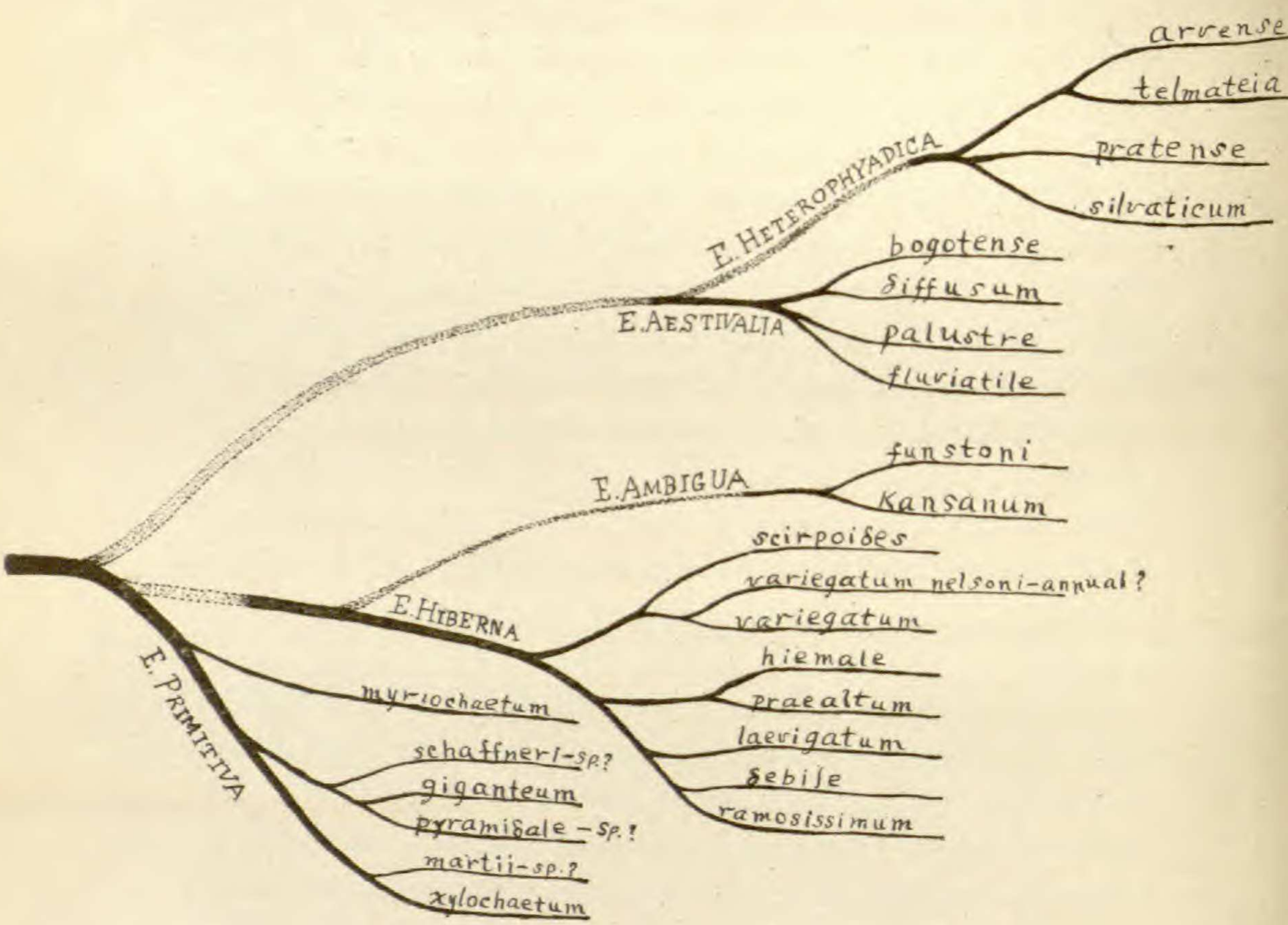
they are still hollow, while in *E. bogotense,* the small main stems are solid. As intimated above, there is a paralleled development to that which has taken place in *E. variegatum* and *E. scirpoides.*

The last group, the *Equiseta heterophyadica,* are apparently a direct offshoot from the main line which ended in the four modern species of the *Equiseta aestivalia.* Like them, they have annual stems and the cones are without points. The sheaths of the main stem are also more or less ampliated. The main evolutionary development consists in the progressive specialization of the fertile shoot, giving a greater and greater dimorphism with the sterile shoot. The four species are *E. silvaticum* L., *E. pratense* Ehrh., *E. telmateia* Ehrh., and *E. arvense* L. All have solid branches having repeated the specialization developed in the higher *Equiseta aestivalia.* In all four species there is a decided loss of chlorophyll in the internodes and usually also in the sheaths of the fertile shoot; and the whorls of branches are disappearing. In the first two species the tips wither after anthesis but in the meantime whorls of green branches begin to develop and the fertile shoot continues as a photosynthetic system. *E. silvaticum* has a prominent specialization in that the branches are usually abundantly compounded, which is a rather rare condition in other species. The two most extreme species are *E. telmateia* and *E. arvense,* both of which show the greatest dimorphism between the sporophyll-bearing shoot and the sterile shoot. The very short-lived fertile shoot has not only lost its chlorophyll or the most of it, but also its branching habit, thus repeating the condition so prominently evolved in the *Equiseta hiberna* and *Equiseta ambigua,* while the sterile shoot retains the prominent system of whorled branches. Both the hered-

itary factors and the response of these factors to internal functional states as well as to the external environment in the expression of morphological characters are very complex. The evolutionary progression in the fertile shoot is shown by comparing *E. fluviatile* with *E. silvaticum* and *E. pratense* as intermediate types and with *E. telmateia* and *E. arvense* as the extreme culmination. *E. telmateia* has highly specialized branches and branch sheath teeth, which have double keels and it is much larger than *E. arvense.* The latter is appropriately placed as the culmination type because it shows the same tendencies of reduction in size as do the extreme species of *Equiseta hiberna* and *Equiseta aestivalia.* There is also a tendency in these most highly specialized fertile shoots to eliminate the stomata and in *E. telmateia* the stomata are sometimes entirely lacking on the internodes.

It is interesting to note, therefore, that in these highly evolved horsetails the aerial shoots show the same kind of progressive evolutionary differentiation as do the leaves of some ferns and the seed plants. There is a progressive series from the condition where there is no difference between the vegetative characters of sporophylls and foliage leaves to the extreme condition of dimorphism in which the sporophyll loses its photosynthetic activity and green color almost entirely as well as other, morphological characters possessed by the foliage leaf. Examples of such progressive differentiation series are seen in passing from *Todea barbara* through *Osmunda claytoniana* to *Osmunda cinnamomea,* or from *Polypodium virginianum* or *Dryopteris marginalis* through *Polystichum acrostichoides* to *Onoclea sensibilis,* where the same type of dimorphism appears between the sporophylls and foliage leaves as is so prominent in the Gymnosperms and the Anthophyta.



LINES OF EVOLUTION IN EQUISETUM

Comparing *E. arvense* with the primitive *E. xylochaetum* or *E. giganteum*, therefore, shows the following six progressive evolutionary advances in fundamental characters: (1) The aerial shoot passes from the perennial to the annual condition; (2) the fertile shoot changes from an abundantly branched condition to a specialized stem without branches; (3) the green fertile shoot is differentiated until it possesses brown internodes, sheaths, and cones through the loss of all or nearly all its chlorophyll; (4) the fertile shoot is very short-lived, soon withering, as compared with the sterile shoot; (5) the cone is more definitely determinate and does not develop a point at the tip; (6) the cone evolves from the condition in which it is nearly sessile or very short-stalked in the highest vegetative sheath to an advanced condition with a rather prominent peduncle having a specialized, reduced, calyx-like sheath just below the lowest whorl of sporophylls. This structure may represent a whorl of sterilized sporophylls. If so, it would have to be regarded as a true perianth. It is perfectly plain, therefore, that from an evolutionary point of view, *Equisetum telmateia* and *E. arvense* are the highest living horsetails and *E. xylochaetum* and *E. giganteum* the lowest.

In agreement with the relationships and series outlined above, the phyletic classification can be shown graphically as a branching system as in the accompanying diagram.

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